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University of South Bohemia in České Budějovice
Faculty of Science

The role of species traits in predator-prey interactions and food web structure

Ph.D. Thesis

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České Budějovice 2012

This thesis should be cited as:
Klečka, J., 2012: The role of species traits in predator-prey interactions and food web structure. Ph.D. Thesis. University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 171 pp.

Annotation

This thesis deals with the role of species traits in predator-prey interactions and food web structure. I conducted laboratory experiments with predatory aquatic insects and their prey to reveal the traits determining who eats whom in small standing waters. I also focused on the possibility of incorporating the observed dependence of predator-prey interactions on body mass into existing food web models. Further, I developed a simple simulation model to explore the consequences of body mass dependent feeding and dispersal for food web assembly. Last, I show that four common methods for sampling aquatic insects differ in their selectivity, especially on the basis of body mass of sampled insects. In conclusion, I combined laboratory experiments, field work and mathematical models to evaluate the importance of body mass and other species traits, such as foraging behaviour and microhabitat selectivity, in predator-prey interactions and explored selected food web level consequences.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 20.12.2012 ....

Jan Klečka

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Entomology, Biology Centre of the ASCR, supporting doctoral studies in the Biology of Ecosystems study programme.

Financial support

The study was supported by the Grant Agency of the University of South Bohemia (grant no. GAJU 145/2010/P) and ERASMUS scholarship partly covering my stay at the University of Sheffield, UK. Further support was provided by the EU Marie Curie European Reintegration Grant 'AquaMod' (PERG04-GA-2008-239543) and by the Grant Agency of the Czech Republic (P505/10/0096) to David S. Boukal.

Acknowledgements

I would like to thank my supervisor David S. Boukal for his guidance during nine long years since my first high school science project until the end of my university studies culminating by the completion of my PhD thesis. I am especially grateful to Andrew P. Beckerman for introducing me to food web theory and for his kind help and stimulating discussions during my six months long stay at the University of Sheffield. This experience has been instrumental for my professional as well as personal development. Many thanks to Kylie Yarlett, Aaron Thierry and their dogs Biffy and Sabah who took care of my well-being in Sheffield and to other members of Andrew's lab. I am also indebted to my parents who stimulated my interest in biology since I was a child and provided me with a lot of patience and personal support. Last, I would like to thank my wife Irena, who has always been helpful and patient and cheered me up when I felt unproductive. She has also been a pleasant collaborator and made me believe that it is possible to achieve a satisfying work-life balance. Thank you!

List of papers and author's contribution

The thesis is based on the following papers (listed thematically):

I. **Klecka, J.** & Boukal, D.S. (2012) Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *PLoS ONE*, **7**, e37741. (IF_{2011} = 4.092, 5-year IF_{2011} = 4.537).
Jan Klečka conducted the experiments, carried out most of the review of published experiments, analysed the data and wrote the manuscript together with David S. Boukal.

II. **Klecka, J.** & Boukal, D.S. (revised version under review) Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study. *Journal of Animal Ecology*. (IF_{2011} = 4.937, 5-year IF_{2011} = 4.971).
Jan Klečka conducted the experiments, analysed the data with the help of David S. Boukal and wrote the manuscript together with David S. Boukal.

III. **Klecka, J.** & Boukal, D.S. (submitted) Anti-refuge effect of aquatic vegetation for planktonic prey. *Biology Letters*. (IF_{2011} = 3.762, 5-year IF_{2011} = 4.049).
Jan Klečka conducted the experiments, analysed the data and wrote the manuscript together with David S. Boukal.

IV. **Klecka, J.** (submitted) Niche model and the size structure of food webs. *PLoS ONE*. (IF_{2011} = 4.092, 5-year IF_{2011} = 4.537).
Jan Klečka developed the model, run the simulations, analysed the data and wrote the manuscript.

V. **Klecka, J.**, Boukal, D.S. & Beckerman, A.P. (manuscript) Body mass dependent dispersal and feeding constraints drive food web assembly.
Jan Klečka developed the model with the help of Andrew P. Beckerman and David S. Boukal, run the simulations, analysed the data and wrote the current version of the manuscript with the help of Andrew P. Beckerman.

VI. **Klečka, J.** & Boukal, D.S. (2011) Lazy ecologist's guide to water beetle diversity: which sampling methods are the best? *Ecological Indicators*, **11,** 500-508. (IF_{2011} = 2.695, 5-year IF_{2011} = 3.021).
Jan Klečka conducted the field work, processed most of the samples, carried out most of the data analysis and took part in writing the manuscript.

I declare that I had a major contribution to all papers as described above.

České Budějovice, 20.12.2012 ....

Jan Klečka

Contents

Chapter I.

Introduction

Introduction

Communities of plants and animals are organized into networks of interacting species. It is extremely challenging to study these complex systems in their entirety. Individual studies thus usually focus on a subset of interactions. Food webs comprising predators and their prey, plant herbivore webs, plant-pollinator networks and other types of ecological networks are thus studied separately. There is a handful of exceptional studies attempting to combine different types of interactions to get a more complete view of the tangle of interspecific interactions in natural communities (Melián *et al.* 2009; Amundsen *et al.* 2009; Pocock, Evans, & Memmott 2012). In this thesis I am dealing with the most traditionally studied type of ecological networks – food webs. Food webs contain only interactions between consumers and their prey and frequently focus on true predator-prey interactions; which is also the case of my thesis. The study of food webs can be approached from many different angles. In my thesis, I use mainly simple laboratory experiments which can help us identify key traits of predators and prey that are responsible for deciding which of the many potential interactions are realised. I use predatory aquatic insects as a highly suitable model group of predators to address the role of species traits in predator-prey interactions. I combine these experiments with simple stochastic food web models. These models provide a rather crude representation of food webs but they can be used to address the consequences of the structure of food webs for their dynamics and stability.

Why to study food webs?

The complexity of food webs reminds us that no species exists on its own and that we need to study interspecific interactions to understand the organizational principles of natural communities. Trophic interactions have to be considered in efforts to understand community build up after restoration of damaged habitats (Tylianakis *et al.* 2008; Memmott 2009; Henson, Craze, & Memmott 2009), colonization of islands (Gravel *et al.* 2011) or species loss due to cascading effects of habitat destruction and climate change (Melian & Bascompte 2002; Petchey *et al.* 2004, 2008b; Woodward *et al.* 2010; Stouffer & Bascompte 2010; O'Gorman *et al.* 2011; Brose *et al.* 2012). Understanding the drivers of predator-prey interactions is thus important not only for our understanding of the structure of communities of interacting species but also for their efficient conservation.

Food web structure is a key to understand food web stability

Theoretical studies of food web stability focused on the relationship between complexity and stability for several decades. May (1972, 1973) used models of food webs where interactions were assigned at random to show that increasing complexity (i.e. connectance and species richness) decreases dynamical stability of model food webs. These results contradicted the fact that natural communities are complex but relatively stable. One of the limitations of May's approach was that he assumed that species interact at random (May 1972, 1973). Recent results demonstrated that stability of large complex food webs may be stem from non-random features of the interactions among species. For example, skewed distribution of interaction strengths with a few strong and many weak interactions seems to increase food web stability (McCann, Hastings, & Huxel 1998;

McCann 2000). Body mass ratios of predators and prey in food webs may affect stability (Brose, Williams, & Martinez 2006b; Heckmann *et al.* 2012) because interaction strength scales with body mass (Emmerson & Raffaelli 2004; Berlow *et al.* 2009). Other features of food web topology, e.g. compartmentalization (Stouffer & Bascompte 2011), also affect food web stability. Hence, an increasing amount of evidence suggests that the key to food web stability lies in non-randomness of food web structure.

After the availability of empirical data on food web structure has increased during last two decades, it becomes apparent that the pattern of interactions in real food webs is by no means random. It has been proposed that there is a feeding hierarchy in food webs in which species can be sorted such that each consumer feeds on species placed lower in that hierarchy. This idea is a basis of a famous cascade model (Cohen, Briand, & Newman 1990). A remarkable feature of the cascade model is that it takes only two parameters, species richness and connectance, and predicts food web structure based on a simple assumption that predators can feed on a limited range of prey (in this case on prey placed lower in the feeding hierarchy). Further development of food web models has led to a new stochastic structural food web model, the niche model (Williams & Martinez 2000), which has been very successful in capturing structural features of real food webs (Williams & Martinez 2000, 2008). Better fit of the niche model compared to the cascade model is the result of an assumption that predators feed on prey placed in a contiguous section of a single axis along which all species can be sorted. It has been speculated that this axis, called the niche axis, might correspond to body mass (Williams & Martinez 2000; Woodward *et al.* 2005). A number of modifications has been proposed to further improve the fit of the niche model (Stouffer, Camacho, & Amaral 2006; Allesina, Alonso, & Pascual 2008; Williams, Anandanadesan, & Purves 2010). All these models belong to a group of stochastic structural food web models. Their major feature is that they use a simple set of phenomenological rules to generate an artificial food web but they do not provide a mechanistic explanation of food web structure (Petchey *et al.* 2011).

Explaining food web structure mechanistically is a challenging task which has been recently approached by applying traditional concepts of optimal foraging theory (Charnov 1976; Stephens & Krebs 1986) at the food web level. A model assigning feeding interactions based on the assumption that predators select the most profitable prey, the diet breadth model of Beckerman, Petchey, & Warren (2006) successfully predicted connectance in real food webs. Its modification assuming four empirically and theoretically justified allometries: 1. abundance on body mass, 2. prey energy content on its mass, 3. attack rate on predator and prey mass, and 4. handling time on predator and prey mass, correctly predicted up to 65% of feeding links in real food webs (Petchey *et al.* 2008a). It suggests that explaining food web structure may be possible by using information on the effects of species traits, such as body mass, on their interactions.

Explaining food web structure by traits of interacting species

The importance of species traits has been recognized in ecology for a long time. The effect of body mass on predator-prey interactions is one of the classic examples (Elton 1927). The interest in the role of body size in food webs has been greatly rejuvenated thanks to the emergence of the metabolic theory of ecology (Brown *et al.* 2004) because the scaling of metabolic rates has implications for consumer-resource interactions. For example, allometric scaling of metabolic rates affects the energy flow between predators and prey of different sizes (Heckmann *et al.* 2012). This effect scales up to the level of large food webs and leads to the dependence of food web stability on predator-prey body mass ratios (Brose *et al.* 2006b; Heckmann *et al.* 2012). Empirical data on interaction strength support these results and show that interaction strength has a highly skewed distribution and that interaction strength depends on body mass (Emmerson & Raffaelli 2004; Berlow *et al.* 2009). The parameters of functional responses have also been shown to depend allometrically on body mass of predators and their prey (Vucic-Pestic *et al.* 2010; Rall *et al.* 2012), although there is a lot of residual variation which could be possibly explained by other species traits. Analysis of a large database of empirical data on predator-prey interactions identified a general allometry of prey mass increasing with predator mass (Brose *et al.* 2006a). Recent more detailed analyses show that the allometry differs between different types of consumers and prey and between different habitats (Bersier & Kehrli 2008; Naisbit *et al.* 2011; Riede *et al.* 2011). This hints at a possibility that some other species traits, such as foraging mode of the predators, affect the allometry (Wirtz 2012). Identifying other traits driving predator-prey interactions apart from body mass is one of the key tasks for the research of predator-prey interactions; gaining such detailed information could be accomplished using controlled laboratory experiments.

Testing the role of species traits in laboratory experiments

Laboratory experiments have been instrumental in the development of our understanding of the factors driving predator-prey interactions. Both predators and their prey can be characterized by various morphological and behavioural traits, which can affect the set of prey consumed by a given predator and modify interaction strength. Some predators forage more easily in certain habitats and prey vulnerability to predation may be greatly affected by morphological and behavioural adaptations (Miner *et al.* 2005; Kishida *et al.* 2009; Toledo, Sazima, & Haddad 2011). The role of body mass in predator-prey interactions is well established (Brose *et al.* 2006a; Bersier & Kehrli 2008; Naisbit *et al.* 2011; Riede *et al.* 2011) but the importance of other traits is much less known. Available data show that the activity and foraging behaviour of predators may affect prey selectivity (Allan, Flecker, & McClintock 1987a; Downes 2002; Wirtz 2012). However, other traits have not been quantitatively evaluated so far.

Predatory aquatic insects are a suitable model group of predators to test the role of species traits in predator-prey interactions because they vary in morphology, foraging behaviour, activity and microhabitat use (reviewed in Peckarsky (1982, 1984)). Many studies focused on predator selectivity (reviewed in Klecka & Boukal (2012)); while earlier results suggested that most predators are generalists, more recent results show that they are selective (Klecka & Boukal 2012). It is likely that their selectivity is driven by predator and prey traits. However, comparative studies testing the role of species traits in predator prey interactions have been very rare, except for tests of the role of body mass. Many early studies (reviewed in Peckarsky (1982, 1984)) reported that these predators do not select prey by size, however, a number of more detailed recent studies has clearly shown that these predators are indeed size-selective (Pastorok 1981; Allan *et al.* 1987a; Allan, Flecker, & McClintock 1987b; Streams 1994). There is also evidence that foraging mode of predators (ambush or searching) and prey activity affect diet composition of predatory aquatic insects (Peckarsky 1982, 1984; Allan *et al.* 1987b; Woodward & Hildrew 2002). Our understanding of the general importance of different species traits for predator-prey interactions is still fragmentary, however, laboratory experiments with suitable species, such as aquatic insects, can help us identify these traits and quantify their effects on the strength of predator-prey interactions. Such data could be used to inform modellers about traits that could be included in a new generation of multiple-trait models of food web structure (Rohr *et al.* 2010; Rossberg *et al.* 2010).

Objectives of the thesis

This thesis deals with the effects of predator and prey traits on predator-prey interactions and food web structure and assembly. I carried out laboratory experiments and built simple simulation models with the overall aim to improve our understanding of the role of body mass, foraging behaviour and other traits for predator-prey interactions and food web structure.

Results of laboratory experiments with predatory aquatic insects and their prey are presented in Chapter II. Paper I. deals with prey selectivity of predatory aquatic insects. We conducted multiple-choice predation experiments using nine species of predators and complemented them with literature survey of similar experiments. The major aim of this paper is to quantify prey selectivity of different predators, identify key prey species and test for ontogenetic diet shifts. We also ask whether there is evidence for a trophic separation of a benthic and a pelagic (or planktonic) module. In Paper II. we further explore the effects of microhabitat association of predators and prey for the strength of predator-prey interactions. We test the role of habitat structure (artificial vegetation) for the mortality of different prey species offered to several predatory aquatic insects. We provide a conceptual summary of the previously observed and expected effects of habitat structure on mortality of prey and test whether the effect of aquatic vegetation depends on microhabitat association of predators and prey. Paper III. tests the role of foraging traits of predators and vulnerability traits of prey for size-dependent predation. Specifically, we ask whether prey-predator body mass allometry is modified by these traits, e.g. whether predators with different foraging behaviour prefer prey of different sizes. We then fit several versions of two recent mathematical models (Rohr *et al.* 2010; Rossberg *et al.* 2010) to test the effect of multiple traits of predators and prey on prey mortality.

Chapter III. focuses on modelling food webs. In Paper IV. I use a body mass based version of a prominent stochastic food web model, the niche model, to compare size structure of model food webs to empirical data on predator-prey body mass ratios and prey-predator body mass allometry. I further modify the model to explicitly incorporate allometric dependence of optimal prey mass on predator mass and add another trait modifying the optimal prey size for predators. The purpose of these modifications is to develop a simple stochastic model of food web structure that could be used in simulation studies to test the role of size structure for food web dynamics. Paper V. deals with food web assembly, i.e. with the temporal development of food webs in new habitats which are colonized from a source species pool. To study food web assembly, we built a modelling framework which incorporates realistic food web structure and body mass dependent dispersal. We use empirically and theoretically justified allometries of abundance and dispersal rate with body mass to simulate the assembly of food webs in new habitats. We test how the speed of food web assembly and temporal changes of food web structure depend on the scaling of dispersal rates with body mass.

Paper VI. in Chapter IV. presents a comparison of four common sampling methods in terms of their selectivity using a large dataset on water beetles. We test whether these methods provide comparable estimates of community composition and whether they are size selective. We also compare the efficiency of the sampling methods based on time investment and simulate rapid surveys from the data to test if it is possible to gain good estimates of local species richness without the need for a long-term sampling campaign.

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Chapter II.

Laboratory experiments

Paper I.

Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects

Klecka, J. & Boukal, D.S. (2012) *PLoS ONE*, 7, e37741

Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects

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Abstract

Predatory aquatic insects are a diverse group comprising top predators in small fishless water bodies. Knowledge of their diet composition is fragmentary, which hinders the understanding of mechanisms maintaining their high local diversity and of their impacts on local food web structure and dynamics. We conducted multiple-choice predation experiments using nine common species of predatory aquatic insects, including adult and larval Coleoptera, adult Heteroptera and larval Odonata, and complemented them with literature survey of similar experiments. All predators in our experiments fed selectively on the seven prey species offered, and vulnerability to predation varied strongly between the prey. The predators most often preferred dipteran larvae; previous studies further reported preferences for cladocerans. Diet overlaps between all predator pairs and predator overlaps between all prey pairs were non-zero. Modularity analysis separated all primarily nectonic predator and prey species from two groups of large and small benthic predators and their prey. These results, together with limited evidence from the literature, suggest a highly interconnected food web with several modules, in which similarly sized predators from the same microhabitat are likely to compete strongly for resources in the field (observed Pianka's diet overlap indices >0.85). Our experiments further imply that ontogenetic diet shifts are common in predatory aquatic insects, although we observed higher diet overlaps than previously reported. Hence, individuals may or may not shift between food web modules during ontogeny.

Paper II.

Anti-refuge effect of aquatic vegetation for planktonic prey

Klecka, J. & Boukal, D.S. (submitted) *Biology Letters*

Anti-refuge effect of aquatic vegetation for planktonic prey

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Summary

Structurally complex habitats are generally thought to decrease predation risk as they provide refuges for prey or hinder foraging activity of predators. We experimentally tested the effect of habitat structure on prey mortality in aquatic invertebrates. The effect of the presence of vegetation on prey mortality depended on predator and prey microhabitat use. Contrary to the prevailing expectations, we observed an anti-refuge effect of vegetation: in the presence of plants, phytophilous predators that perched on the plants imposed higher predation pressure on planktonic prey; at the same time, mortality of benthic prey decreased. Predation by benthic and planktonic predators on either type of prey remained unaffected by the presence of vegetation. Our results demonstrate that the effects of habitat structure on predator-prey interactions are more complex than simply providing refuges and may both decrease and increase prey mortality depending on microhabitat use and behaviour of predators and prey.

Keywords: predation, predator-prey interactions, habitat complexity

Paper III.

Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study

Klecka, J. & Boukal, D.S. (revised version under review) ***Journal of Animal Ecology***

Foraging and vulnerability traits modify predator-prey body mass allometry: freshwater macroinvertebrates as a case study

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Running headline: Predator-prey body mass allometry

Summary

1. Predation is often size selective but the role of other traits of the prey and predators in their interactions is little known. This hinders our understanding of the causal links between trophic interactions and the structure of animal communities. Better knowledge of trophic traits underlying predator-prey interactions is also needed to improve models attempting to predict food web structure and dynamics from known species traits.
2. We carried out laboratory experiments with common freshwater macroinvertebrate predators (diving beetles, dragonfly and damselfly larvae and water bugs) and their prey to assess how body size and traits related to foraging (microhabitat use, feeding mode and foraging mode) and to prey vulnerability (microhabitat use, activity and escape behaviour) affect predation strength.
3. The underlying predator-prey body mass allometry characterizing mean prey size and total predation pressure was modified by feeding mode of the predators (suctorial or chewing). Suctorial predators fed upon larger prey and had ~3 times higher mass-specific predation rate than chewing predators of the same size, and may thus have stronger effect on prey abundance.
4. Strength of individual trophic links, measured as mortality of the focal prey caused by the focal predator, was determined jointly by the predator and prey body mass and their foraging and vulnerability traits. In addition to the feeding mode, interactions between prey escape behaviour (slow or fast), prey activity (sedentary or active) and predator foraging mode (searching or ambush) strongly affected prey mortality. Searching predators were ineffective in capturing fast-escape prey in comparison to the remaining predator-prey combinations, while ambush predators caused higher mortality than searching predators and the difference was larger in active prey.
5. Our results imply that the inclusion of the commonly available qualitative data on foraging traits of predators and vulnerability traits of prey could substantially increase biological realism of food web descriptions.

Key-words: allometry, aquatic insects, Heteroptera, Dytiscidae, Odonata, feeding, foraging, predation, trophic traits

Chapter III.

Modelling food webs

Paper IV.

Niche model and the size structure of food webs

Klecka, J. (submitted) *PLoS ONE*

Niche model and the size structure of food webs

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Abstract

The structure of food webs is frequently described using stochastic models. A prominent example, the niche model, was found to produce artificial food webs that resemble the structure of real food webs according to comparisons of a range of summary statistics between model-generated and real food webs. However, the size structure of food webs generated by the niche model and real food webs has not yet been rigorously compared. To fill this void, I use a body mass based version of the niche model and compare the prey-predator body mass allometry and predator-prey body mass ratios predicted by the model to empirical data. The results show that the model predicts weaker size structure than observed in real food webs. I further describe modifications of the niche model that include empirical prey-predator mass allometry which controls optimal prey mass for predators. Optionally, optimal prey mass can also depend on a second predator trait, such as foraging mode. These empirically motivated modifications of the niche model produce artificial food webs that have similar values of summary statistics as the niche model but allow for more realistic representation of the size structure of real food webs. These modifications of the niche model can be used to generate artificial food webs varying in several aspects of size structure in a controlled way. Although these models invoke no specific mechanisms to *explain* the structure of food webs, they provide new opportunities for simulating the consequences of size structure for food web dynamics and stability.

Paper V.

Body mass dependent dispersal and feeding constraints drive food web assembly

Klecka, J., Boukal, D.S. & Beckerman, A.P. (manuscript)

Body mass dependent dispersal and feeding constraints drive food web assembly

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Abstract

Food webs are often described as static networks of interacting species and little attention has been devoted to research of food web assembly and temporal dynamics. On the other hand, studies of community assembly have usually avoided complex food web structure and assumed random species-invariant dispersal and discrete trophic levels. We built a modelling framework to study food web assembly which incorporates realistic food web structure and body mass dependent dispersal. We show that dispersal-body mass scaling and feeding constraints together drive food web assembly. First, the assembly process is slowed down when small and even more when large species have higher colonization rate. This effect is magnified by body mass dependent feeding which affects the probability of successful colonization. Food web structure and body mass distribution also vary systematically during the assembly process and among different dispersal scenarios. Our results demonstrate that the scaling of dispersal rate with body mass fundamentally affects food web assembly with potential implications for community stability during early stages of food web development in newly colonized environments, such as islands or restored habitats. We conclude that future development of the theory of community assembly should bridge the gap between the research of dispersal and extinction-colonization processes on one side and food web structure on the other side.

Chapter IV.

Field sampling methods

Paper VI.

Lazy ecologist's guide to water beetle diversity: which sampling methods are the best?

Klečka, J. & Boukal, D.S. (2011) *Ecological Indicators*, 11, 500-508

Lazy ecologist's guide to water beetle diversity: which sampling methods are the best?

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Abstract
Biodiversity surveys of aquatic macroinvertebrates in standing water rely on various methods, but a thorough comparison of the techniques is lacking. This hampers analyses across surveys and impedes development of efficient sampling schemes. We compare the selectivity and efficiency of four methods commonly used to collect aquatic insects—activity traps (ATs), box trap (BT), handnetting (HN) and light trap (LT) —using a large dataset on water beetles in a site with ~100 species. We propose to use time investment as a natural basis to compare efficiency, since it applies to any method. The results inherently differ from results based on samples or individuals because methods are neither equally demanding nor equally rewarding. Most differences between methods arise from their size selectivity: ATs select for larger species, while HN and BT seem least selective. Attraction to light is taxon-specific and LT yields more depauperate samples than ATs, BT and HN, limiting the use of LT in community studies. To boost the development of cost-effective protocols, we also identify the best designs for rapid bioassesment by simulating short surveys from the data. Combinations of ATs and BT give most species; the results are robust to partitioning of effort between both methods. However, these rapid surveys miss on average more than 40% of all species in our study. Our results therefore emphasize that long-term studies using multiple methods are vital for measuring diversity in species-rich freshwater habitats.

Chapter V.

Conclusions

Conclusions

I presented results of laboratory predation experiments with predatory aquatic insects and their prey, simulation models of food web structure and assembly and a field study testing the selectivity of common sampling methods. The unifying theme of all papers included in my thesis is the role of species traits in predator-prey interactions and their implications for the structure and temporal development of multispecies communities.

Main findings

Results of laboratory experiments show that my model group of predators, aquatic insects, feed selectively (Paper I.). Diet of individual species can be explained by several traits of the predators and their prey. We demonstrate that microhabitat association of predators and prey creates modular structure of aquatic food webs which is surprisingly detectable even in microcosm experiments (Paper I.). Microhabitat association of predators and prey also modifies the effect of habitat structure on predator-prey interactions; we observed an "anti-refuge" effect of aquatic vegetation for planktonic prey which suffers higher mortality in the presence of vegetation, despite the fact that vegetation is usually seen as a source of refuges (Paper II.). We further report that predator foraging and prey vulnerability traits modify prey-predator body mass allometry and affect the strength of predator-prey interactions (Paper III.). These results suggest that it might be possible to explain and predict the structure of food webs by using several species traits.

In a second chapter, I present two simulation studies dealing with food web structure. I demonstrate that a body mass based modification of a prominent food web model, the niche model, generates food webs with weaker size structure than usually observed in real food webs (Paper IV.). I modify this model to include the allometry of optimal prey mass and predator mass; a second predator trait can optionally modify this allometry. Such a model allows us to generate artificial food webs differing in their size structure, which can be used in simulation studies to test the consequences of different aspects of size structure for food web stability. In another study, we tested the role of possible allometric scaling of dispersal rate with body mass for food web assembly (Paper V.). Our simulation model couples realistic food web structure with body mass dependent dispersal to show that the slope of the scaling of dispersal rate with body mass can greatly affect the process of food web assembly in new habitats.

Last, we show that four common methods used to sample aquatic insects differ in their selectivity (Paper VI.). We identified species body mass as a main factor responsible for differences among the four sampling methods. We further show that a long-term sampling campaign is necessary to gain a good estimate of total species richness in a species rich wetland. These results suggest that sampling may be a source of important biases hindering our efforts to understand the structure of natural communities.

Future directions

I demonstrated that a fruitful way towards improving our understanding of food webs may be to combine laboratory experiments, models and field research. Laboratory experiments can deepen our understanding of the mechanisms of prey choice and identify traits of predators and prey underlying the observed predator-prey interactions. Such information can be used to develop new food web models more faithfully describing the structure of real food webs. Detailed information on predator and prey traits will surely be needed to move towards more mechanistic explanations of food web structure. Meanwhile, simple stochastic models can be used to gain better insights into the relationship between food web structure and stability. History shows that food web models need to be informed by high quality data to capture food web structure faithfully. This is a necessary condition for getting the correct answers to the questions the models are supposed to tackle. Food web studies have so far focused mostly on the role of body mass but resolving the role of other traits driving predator-prey interactions and food web structure is an important challenge for the coming years.

Appendix

Curriculum Vitae